

**Two new species of the red alga *Chrysymenia* J. Agardh
(Rhodymeniales: Rhodymeniaceae) from the
tropical western Atlantic**

James N. Norris and David L. Ballantine

(JNN) Department of Botany, NHB 166, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, U.S.A.;

(DLB) Department of Marine Sciences, University of Puerto Rico,
Mayagüez, Puerto Rico 00681, U.S.A.

Abstract.—Two new species of *Chrysymenia*, *C. littleriana* and *C. nodulosa*, are described from subtidal habitats, and compared to worldwide members of their morphological form-group, and to the other species of the tropical western Atlantic. *Chrysymenia nodulosa*, from the southwest coast of Puerto Rico, is characterized by its terete to compressed axes, opposite or alternate pinnate branching to 2 orders, nodulose swellings on the thallus surface, and spermatangia produced in anticlinal rows. *Chrysymenia littleriana*, from southern Martinique, is characterized by compressed axes, opposite pinnate branching to 5 orders, a lack of nodulose swellings, and spermatangia in periclinal rows. Among the known species of *Chrysymenia*, *C. bullosa* is recognized to be a *Botryocladia* and a new combination is proposed. Observations suggest that the ontogeny and structure of spermatangia in species of *Chrysymenia* be investigated as taxonomic characters, possibly for subgeneric groupings.

The red algal genus *Chrysymenia* J. Agardh (1842:105; Rhodymeniaceae Harvey, Rhodymeniales Kylin) is known from temperate to tropical seas. Species of this genus are found from the lower intertidal to the subtidal, sparsely distributed but sometimes locally abundant, and usually growing solitarily or few to several in a stand. The genus *Chrysymenia* is characterized by mucilaginous, fleshy thalli composed of simple or branched axes and branches that are terete, compressed, or nearly flattened, and that are usually hollow throughout. Anatomically, the cavities are bounded by large medullary cells and are mucilage-filled. The medullary cells may lack filaments or issue few to many medullary filaments and bear sessile gland cells. The cavities may be filled in varying degrees with medullary filaments, especially at the base of the stipe or in the flattened branches of some species.

Outward to the medullary cells is a cortex 1–4 cells thick. Tetrasporangia are cruciately divided and scattered between the cortical cells. Cystocarps are scattered, partially immersed, ostiolate, and project above the cortex. Spermatangia are borne in surface areas of the cortex.

The seventeen presently known species of *Chrysymenia* can be divided into three morphological form-groups. Species of form-group 1 have erect thalli that are terete to moderately compressed: *C. ventricosa* (Lamouroux) J. Agardh (1842), *C. vesiculosa* J. Agardh (1851), *C. enteromorpha* Harvey (1853), *C. halymenioides* Harvey (1853), *C. wrightii* (Harvey) Yamada (1932), and *C. grandis* Okamura (1933). Species of form-group 2, have erect thalli that are flattened and blade-like: *C. agardhii* Harvey (1853), *C. digitata* (Harvey) J. Agardh (1876), *C. planifrons* (Melville) J. Agardh (1876), *C.*

dickieana J. Agardh (1892), *C. lobata* Howe (1914), *C. polyglandulosa* Okamura (1930), and *C. ornata* (J. Agardh) Kylin (1931). Species of form-group 3 are repent, with flattened, lobed thalli: *C. kaernbachii* Grunow (1889), *C. procumbens* Weber van-Bosse (1928), *C. okamurai* Yamada & Segawa (1953), and *C. glebosa* Abbott & Littler (1969). Cribb (1983:67) has suggested that the species of form-group 3 are morphologically similar and may prove to be conspecific. *Chrysymenia bullosa*, originally described from the Archipelago of Madeira (Levring 1974) and recently reported from the Azores (Fredericq et al. 1992), we now recognize, because of its solid stipe, to be a *Botryocladia*. Accordingly we propose the following new combination, ***Botryocladia bullosa*** (Levring) J. Norris & Ballantine, comb. nov. [Basionym: *Chrysymenia bullosa* Levring, Bol. Mus. Municipal Funchal 28(125):80, figs. 13–14, 1974].

Currently seven species of *Chrysymenia* are reported from the tropical western Atlantic: *C. agardhii*, *C. dickieana*, *C. enteromorpha*, *C. halymenioides*, *C. planifrons*, *C. ventricosa* (Taylor 1960, Wynne 1986), and *C. cf. okamurai* (reported from Belize by Norris & Bucher 1982). Some of these species had originally been members of the genus *Cryptarachne* (Harvey) Kylin (1931: 11, 1956:331; see also Taylor 1960:480), which was separated from *Chrysymenia* on the basis that the thalli of *Chrysymenia* are generally terete (rarely compressed) and have a central cavity lacking internal rhizoids, whereas the thalli of *Cryptarachne* are compressed to flat and possess internal rhizoids. Some of the species included in *Chrysymenia* by Kylin (1931), however, clearly possess medullary rhizoidal filaments. In discussing *Chrysymenia glebosa*, Abbott & Littler (1969) followed Okamura's (1936) opinion that the presence or absence of medullary rhizoidal filaments is a poor taxonomic character, and thus recognized a single genus.

Herein we describe two new western Atlantic species of *Chrysymenia* with type lo-

calities in Puerto Rico (Greater Antilles) and Martinique (Lesser Antilles).

Materials and Methods

All specimens of *Chrysymenia* were collected by SCUBA diving and liquid-preserved in buffered 5% Formalin-seawater. Hand-cut sections and squash preparations were stained and fixed with 1% acidified aniline blue and mounted in Karo® clear corn syrup, with phenol added as a preservative, on microscope slides (Tsuda & Abbott 1985). Line drawings were prepared with the aid of a camera lucida on an Olympus light microscope. Photomicrographs were taken on a Zeiss Universal microscope using a Zeiss MC-63 with a M-35 camera body and Kodak® TMAX 35 mm B&W film. Specimens, including microscope slides and liquid-preserved material are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution (US); duplicate isotype or paratype specimens are deposited in the Algal Herbarium, University of Puerto Rico, Mayagüez (MSM), the University of Michigan Herbarium (MICH), and the Herbarium of Seoul National University (SNU). Herbarium abbreviations follow Holmgren et al. (1990).

Results

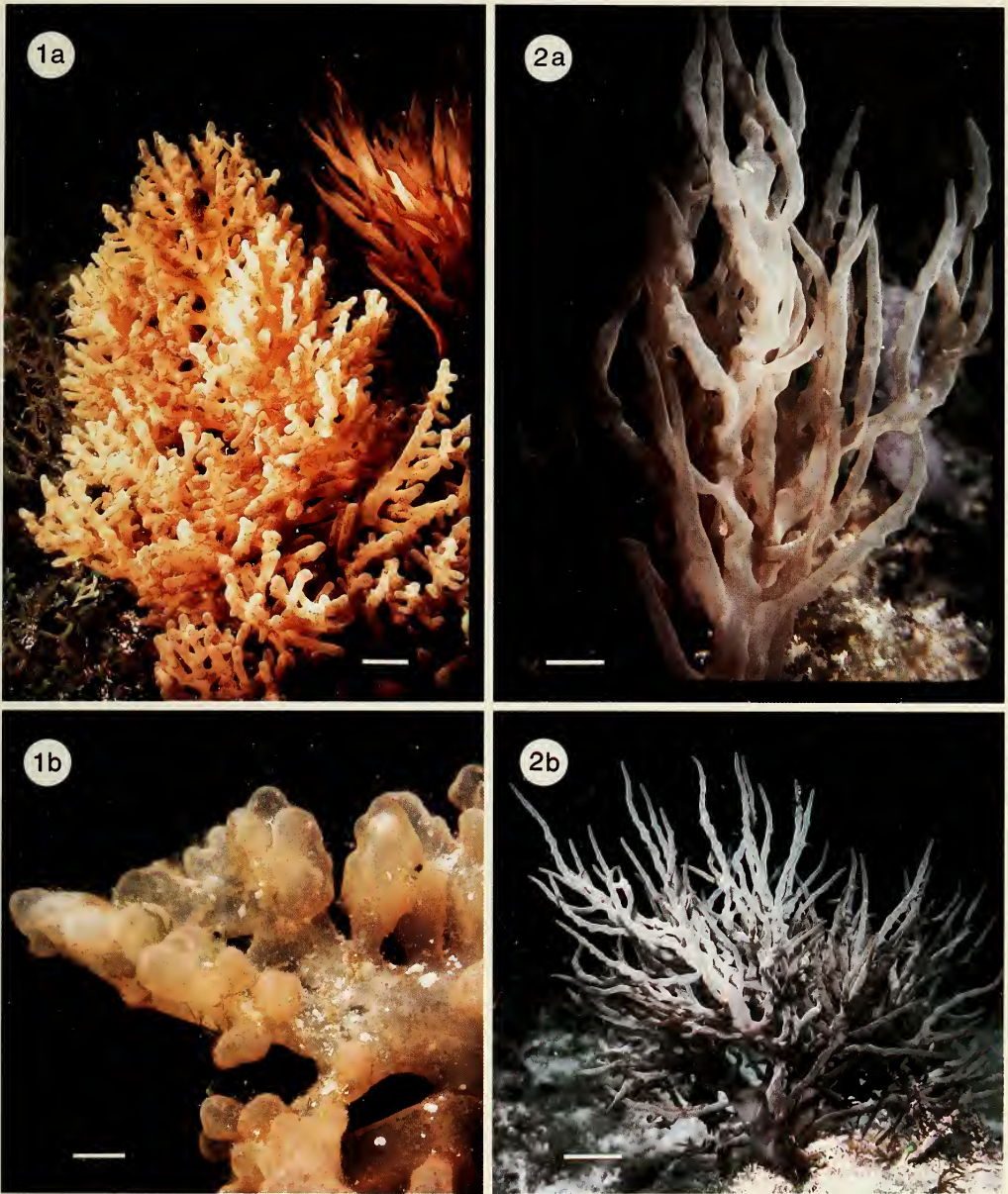
Chrysymenia littleriana

J. Norris & Ballantine, sp. nov.

Figs. 1a, b, 3, 6, 10–14

Latin description. — Thalli erecti usque ad 20 cm alti rufi gelatinosissimi, axe principali brevi (3–5 mm alto) tereti, parte basali compressescenti ad 15 mm lato, per hapteron discoideum affixo, usque ad 3–4(–5) ordines ramosi, filamentis lateralibus oppositis irregulariter pinnatis. Rami ad basin plerumque leviter constricti (interdum aconstricti), saccatescentes elongatescentesque, ad apicem inflati plerumque late obtusati usuque ad 10 mm diam.

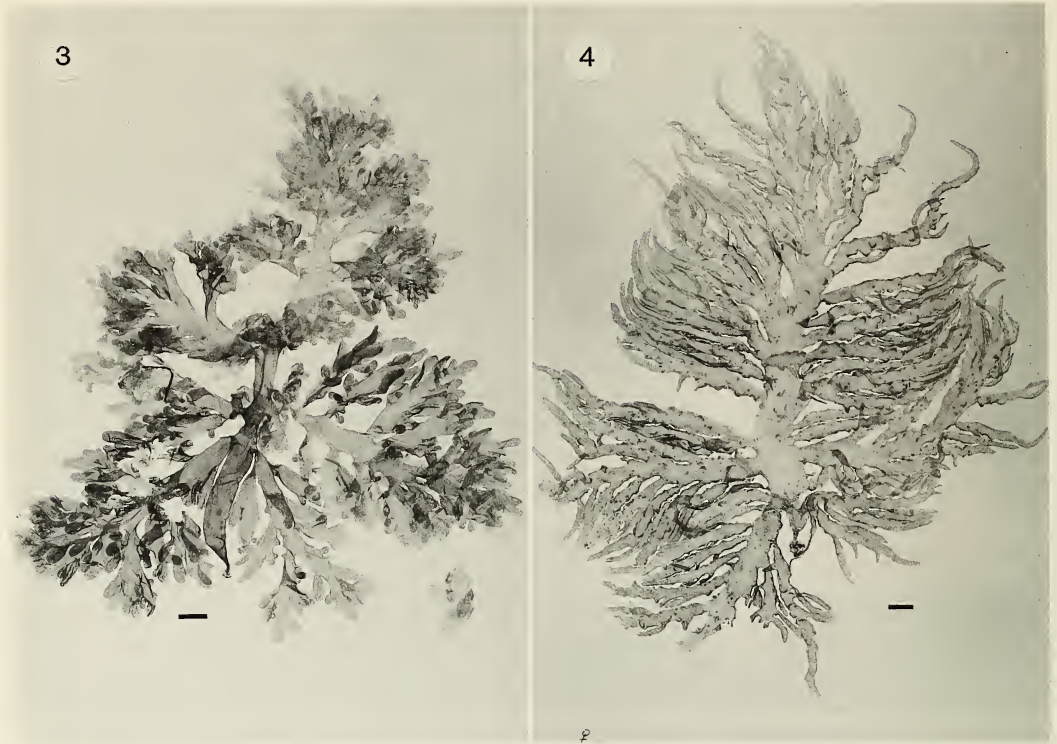
Axes et rami cavati, cavo mucoso, me-



Figs. 1–2. Underwater photographs of the new species of *Chrysymenia* at their type localities. 1, *C. littleriana*, 15 m depth, Diamond Rock, Martinique: a, habit (scale bar = 20 mm); b, close-up of a branch showing the broadly obtuse apices (scale bar = 30 mm). 2, *C. nodulosa*, 17 m depth, Media Luna Reef, La Parguera, Puerto Rico: a, close-up showing the nodulose swellings on the thallus and tapering apices of the branches (scale bar = 20 mm); b, habit (scale bar = 10 mm).

dulla incolorata cellularum 2 aut 3 stratis composita; stratum intimum medullae cellularum irregulariter rotundatarum vel ovalium, usque ad 500 μm diam.; strata externa medullae cellularum anticlinaliter

elongatarum versus exterium decrescentum. Fila rhizoidalia medullosa usque ad 15 μm diam., cellulis medullois intimis genita, aliquando basaliter inflata, interdum localiter abunda. Cavitas ad basin stipitis



Figs. 3-4. Holotype specimens. 3, *Chrysiymenia littleriana*, Alg. Coll. #US-162777 (scale bar = 10 mm); 4, *Chrysiymenia nodulosa*, Alg. Coll. #US-162770 (scale bar = 10 mm).

dense filis rhizoidalibus medullosis repleta, filis inter cellulas medullosas at super hapteron crassiparietibus. Cellulae glandulosae interdum ex cellulis medullosis intimis in cavitatem centram eminentes, pyriformae, usque ad 22-30 μm longae, atrocoloratae 1(-5) in quoque cellula. Cortex tristromaticus, cellulis intimis modice pigmentosis usque ad 25 μm diam., cellulis intermeditis usque ad 15 μm diam., cellulis externis cellulae (1-2) stratis formatae, cellulis manifeste elongatis, ca. 12 μm longis \times 6 μm diam.

Tetrasporangia cruciata elliptica, ca. 25 μm longis \times 16 μm diam., ex cellulis corticis intiis orta. Spermatangia in soros superficiales dispositis, rotunda vel ovalia, 2-3 μm lata, in catenas periclinales (1-2-3(-4)) per cellula parentales spermatangiorum effertia. Cystocarpia prominentia thaliformia,

pericarpio crasso, in partibus distabilis thalli dispersa.

Description. —Thalli erect, to 20 cm tall, reddish-mahogany, highly gelatinous, with a short, terete main axis, 3-5 mm long, the basal portion becoming compressed, to 15 mm in diam., attached below by a discoidal holdfast, the thallus branched 3 to 4(-5) orders, with opposite, irregularly pinnately branched lateral branches. Branches at their base usually slightly constricted (occasionally not constricted), becoming saccate and elongated, and terminating in inflated, usually broadly obtuse apices up to 10 mm in diam.

Axes and branches hollow and mucilage-filled with a medulla composed of 2 or 3 layers of colorless cells; innermost layer of cells irregularly roundish to oval, up to 500 μm diam.; outer medullary cells decreasing



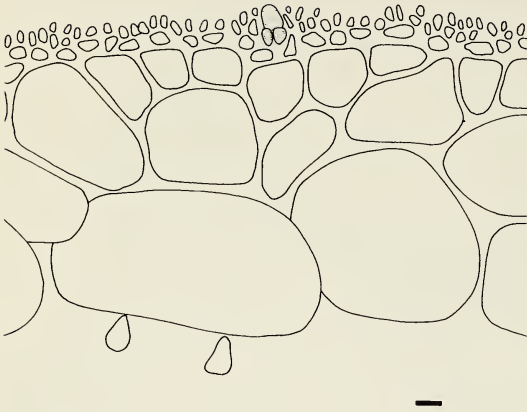
Figs. 5–6. Transverse sections through the prominent cystocarps. 5, hemispherical cystocarp of *C. nodulosa*, note the fusion cell (scale bar = 50 μm); 6, dome-shaped cystocarp of *C. littleriana* with mature carposporangia (scale bar = 100 μm).

sharply in size towards the exterior and anticlinaly elongated. Medullary rhizoidal filaments up to 15 μm diam., issuing from the innermost medullary cells, occasionally inflated at the origin, sometimes locally abundant. Cavity of the lowermost basal portion densely filled with medullary rhizoidal filaments that also grow around and between the medullary cells, and these are thick-walled above the holdfast. Gland cells occasional on the innermost medullary cells

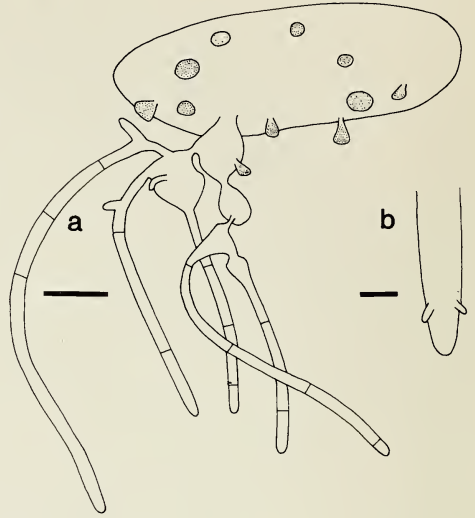
facing into the central cavity, pyriform, to 22 μm by 30 μm , darkly staining, and usually 1(–5) per cell (Fig. 11). Cortex composed of 3 cell layers, an innermost layer of lightly pigmented cells up to 25 μm diam., an intermediate layer of cells up to 15 μm diam., and an outer layer of (1–)2 distinctly elongate cortical cells, averaging 12 μm long by 6 μm in diam.

Tetrasporangia cruciate, elliptical, ca. 25 μm by (12.5–)16 μm , and cut off by inner-

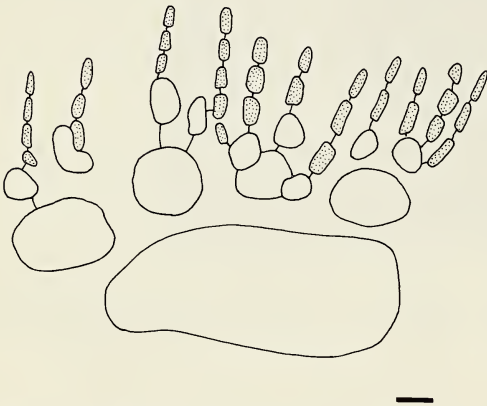
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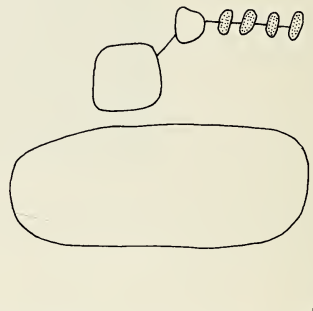
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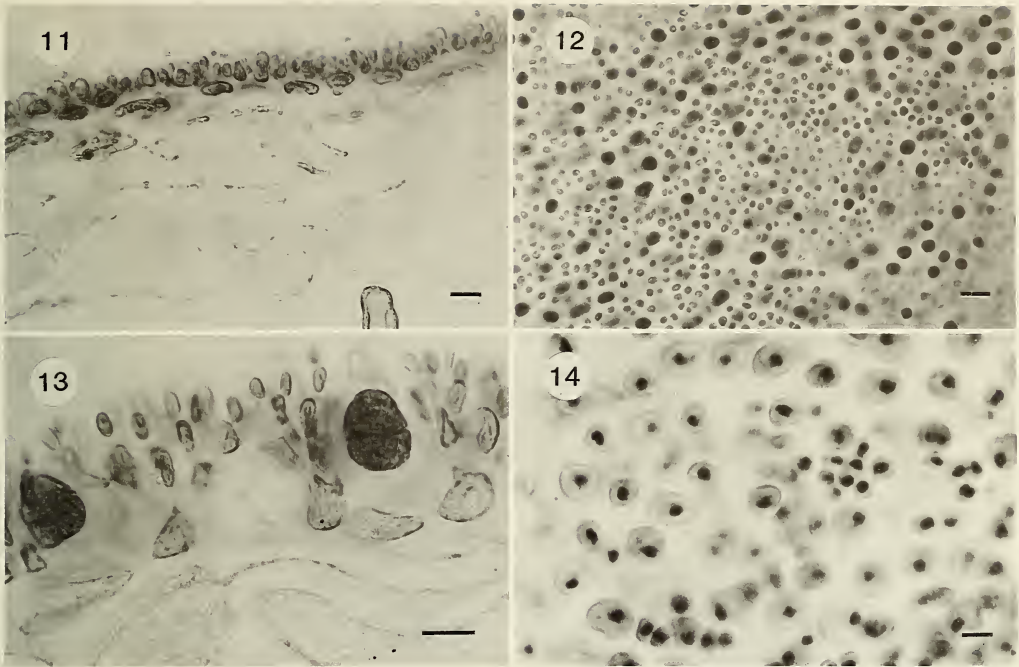


Figs. 7–8. Anatomy of *C. nodulosa*. 7, transection through a tetrasporangial thallus; note the cruciate tetraspore in the outer cortex, and the gland cells borne on large cells of the inner medulla (scale bar = 25 μm); 8a, inner medullary cell from near the base showing numerous gland cells and developing medullary filaments (scale bar = 100 μm); 8b, end of a medullary filament showing two small papillate projections (scale bar = 20 μm).

Figs. 9–10. Transection through spermatangial sori. 9, cortex of *C. nodulosa* showing spermatangial parent cells with one to four spermatia cut off in anticlinal series (scale bar = 15 μm); 10, *C. littleriana* showing spermatangial parent cell with spermatia cut off in periclinal series (scale bar = 15 μm).

most cortical cells (Fig. 13). Spermatangia in sori on thallus surface (Fig. 12). Spermatangial parent cells produce in periclinal chains (1–)2–4 spermatangia, spherical to

oval, 2–3 μm in diam. (Figs. 10, 14). Cystocarps prominent, up to 1.2 mm dome-shaped, scattered over the distal portions of the thallus, with a thick pericarp (Fig. 6).



Figs. 11–14. Anatomy of *C. littleriana*. 11, transection showing outer cortex and inner medulla with a single large gland cell (scale bar = 25 μm); 12, surface view of spermatangial sorus (scale bar = 10 μm); 13, transection through a tetrasporangial thallus showing cruciate tetraspores in outer cortex (scale bar = 15 μm); 14, surface view showing spermatia in periclinal rows above the spermatangial parent cell (scale bar = 5 μm).

Holotype. —DML-746 (Alg. Coll. US-162777), including liquid-preserved specimens and accompanying microscope slides; leg. C. Forsyth, B. L. Brooks, M. M. Littler & D. S. Littler, 20 Jul 1986 (Fig. 3).

Type locality. —Attached to rock, ca. 8 m depth, Diamond Rock (14°26'60"N, 61°02'50"W), Martinique, French West Indies, Lesser Antilles.

Paratypes. —All from the type locality, attached to basalt rock, 12–15 m depth, Diamond Rock, DML-17092 (Alg. Coll. US-162662), 21 May 1989, leg. D. S. Littler, M. M. Littler, B. L. Brooks & S. A. Reed, 21 May 1989; and, DML-17223 ♀, ♂, & ⊕ (Alg. Coll. US-162775; MSM; MICH; SNU), leg. B. L. Brooks, S. A. Reed, D. S. Littler & M. M. Littler, 23 May 1989.

Etymology. —*Chrysymenia littleriana* is named for our colleagues, Diane S. Littler and Mark M. Littler (National Museum of

Natural History, Smithsonian Institution) in recognition of their phycological contributions and having collected this distinctive alga; in choosing the Latin adjectival, *-iana*, the specific name translates as “the Littlerian *Chrysymenia*.”

Chrysymenia nodulosa

J. Norris & Ballantine, sp. nov.

Figs. 2a, b, 4, 5, 7, 8a, b, 9

Latin description. —Thalli erecti, usque ad 30 cm alti, cinerascetes gelatinosi, stipitibus brevibus, axibus ramisque juventute fere omino teretibus, usque ad 6 mm diam. leviter nodulosis aetate compressescentibus usque ad 12 mm latis, magis nodulosis, ramificatio oppositis aut alternatis, plerumque plano singulari, ramosis lateralibus pinnatis usque ad 2 ordines.

Axes et rami cavatae, medulla incolorata,

cellularum plerumque 3 stratis composita, cellulis intimis maximis, cellulis extrinsecus decrescentibus. Cellulae medulloasae intimae irregulariter rectangulares, usque ad 300 $\mu\text{m} \times 600 \mu\text{m}$. Fila rhizoidalia medullosa plerumque in partibus veteribus, usque ad 22 μm diam., basaliter tumidis ex cellulis medullosis intimis, plerumque cellulis medullosis aliis, saepe distaliter minute papillosis. Cellulae glandulosae abundantes ex intimis cellulis medullosis in cavitatem centralem eminentibus, pyriformae, usque ad 35 μm longae \times 32 μm diam., atrocoloratae, usque ad 25 in quoque cellula. Cortex bivel tristromaticus, cellulis parvis; pilis in partibus veteribus corticis adundantibus superficie in sicco corno.

Tetrasporangia cruciata, elliptica, 28–36 μm longa \times 14–18 μm diam.; in strato corticali parce dispersa. Spermatangia in soros superficiales dispositis. Spermatangia rotunda vel ovalia 2.2–3.6 μm lata in catenas anticlinales (1–)2–4(–5) per cellulas parentales spermatangiorum efferentia. Cystocarpia prominentia hemirotunda, usque ad ca. 1 mm diam. ad superficiem thalli.

Description.—Thalli erect, up to 30 cm tall above a short stipe, grayish, gelatinous, axes and branches when young almost entirely terete, to 6 mm diameter, and slightly nodulose, becoming compressed, to 12 mm broad, and more nodulose with age and size; branching mostly in a single plane with opposite or alternate, pinnately branched laterals to 2 orders.

Axes and branches internally hollow with a medulla generally of 3 layers of colorless cells which are largest internally and become smaller towards the surface. Innermost medullary cells are irregularly rectangular, up to 300 μm by 600 μm (Fig. 7). Medullary filaments mostly in older portions, to 22 μm in diam. (Figs. 8a, b), inflated at their origin from the innermost medullary cells (Fig. 8a) or occasionally from other medullary cells, and often with small papilla-like projections near distal ends (Fig. 8b). Gland cells (Figs. 7, 8a) are abundant

on innermost medullary cells facing into the central cavity, pyriform, to 35 μm long by 32 μm diam., darkly staining, and up to 25 per cell. Cortex composed of 2 or 3 layers of small cells (Fig. 7); hairs abundant in cortex of older portions of thallus, giving the surface a horny texture when dried.

Tetrasporangia cruciate, oval, 28–36 (–38) μm long by 14–18 (–20) μm wide; sparingly scattered in the cortical layer (Fig. 7). Spermatangia in sori on thallus surface. Spermatangial parent cell produces an anticlinal chain of (1–)2–4(–5) spermatangia, spherical to oval, 2.2–3.6 μm (Fig. 9). Cystocarps protruding, hemispherical, to about 1 mm diam. in surface view (Fig. 5).

Holotype.—DLB-3108, cystocarpic (Alg. Coll. US-162770), leg. D. L. Ballantine, 5 May 1988 (Fig. 4).

Type locality.—17 m depth, 1.5 km seaward of Media Luna Reef, La Parguera, Puerto Rico, Greater Antilles.

Isotypes.—DLB-3108, tetrasporangial (Alg. Coll. US-162772; MSM); and DLB-3108, spermatangial (Alg. Coll. US-162771; MSM; and MICH).

Paratypes.—All from Media Luna Reef, La Parguera, leg. D. L. Ballantine: DLB-1837 (MSM), 24 Jan 1985; DLB-2128 (Alg. Coll. US-014407), 2 Nov 1985; DLB-3340 (MSM), 21 Feb 1989; and DLB-3375 (MSM), 26 Apr 1989.

Etymology.—The specific epithet *nodulosa* refers to the small, knobby swellings on the thallus surface, a characteristic unique to this new species of *Chrysymenia*. It is the diminutive of Latin *nodosus* (Stearn 1973), and means “full of little knobs.”

Key to the Western Atlantic species of *Chrysymenia*

- 1. Thallus flat 2
- 1. Thallus terete to compressed 4
- 2. Branches of the thallus broad (>2.0 cm), foliose 3
- 2. Branches of the thallus narrow (<2.0 cm), irregularly branched to 4(–5) orders *C. dickieana*

- 3. Thallus dichotomous to palmately branched, 2.0 to 2.5 cm broad *C. agardhii*
- 3. Thallus branching irregularly lobed, >2.5 cm *C. planifrons*
- 4. Thallus terete, occasionally compressed at and above the base 5
- 4. Thallus slightly to moderately compressed throughout 6
- 5. Branches highly constricted at the base *C. enteromorpha*
- 5. Branches not or barely constricted at the base *C. ventricosa*
- 6. Branching dichotomous *C. halymenioides*
- 6. Branching pinnate 7
- 7. Thalli with nodulose swellings (more pronounced in older and/or larger thalli) *C. nodulosa*
- 7. Thalli without nodulose swellings *C. littleriana*

Discussion

The genus *Chrysiyenia* has close affinities to *Botryocladia* (J. Agardh) Kylin (1931: 17). These genera are separated by the vegetative characters of solid axes and diaphragms in *Botryocladia* and hollow axes without diaphragms in *Chrysiyenia*. Brodie & Guiry (1988) pointed out that the degree of stipe development in *Botryocladia* is variable. They speculated that the genus might be an artificial grouping of species, but they retained it with reservations. In our specimens, we observed the short, stiptate regions of the new species to be filled with rhizoidal filaments, in some places very densely. This suggests that the nature and origin of the cells in the stipe and axes may be a useful taxonomic character, i.e., the solid, parenchymatous medulla of the axes in *Botryocladia* vs. the rhizoidal filament-filled cavity of the stipe in *Chrysiyenia*.

Chrysiyenia littleriana and *C. nodulosa* have some features in common, including the short stipe above a discoidal holdfast, compressed axes, and pinnate branching

(Figs. 1–4). These new species are also similar anatomically (Figs. 7, 11), with large medullary cells of *C. littleriana* generally in two layers and those of *C. nodulosa* mostly in three layers. Both species have two or three layers of cortical cells, although the outermost cortical cells in *C. littleriana* are elongate (Fig. 13). They both produce non-aggregated gland cells from inner medullary cells (Figs. 7, 8, 11), although they are much more abundantly produced in *C. nodulosa*. In *C. nodulosa*, the medullary filaments frequently possess very minute, papilla-like projections near their distal ends (Fig. 8b) and the inner medullary cells give rise to internal rhizoids that are inflated at their origin (Fig. 8a). Sometimes the internal rhizoids of *C. littleriana* are also similarly inflated. Transections of both *C. littleriana* and *C. nodulosa* through the terete, stipitate basal region reveal cellular medullary and cortical regions similar to the distal portions of inflated thallus branches; however, the central medulla of this region is densely filled with branching, rhizoidal filaments.

Reproductively the cruciately divided tetrasporangia are oval and cut off by an inner cell of the cortical layer in both new species (Figs. 7, 13); however, they are larger in *C. nodulosa* (28–36 μm by 14–18 μm) than in *C. littleriana* (25 μm by 16 μm). Female *C. nodulosa* and *C. littleriana* are readily recognizable by their hemispherical and dome-shaped cystocarps that project well above the thallus surface (Figs. 5, 6).

Lee (1969:figs. 1A, B, 2A, B) recognized two modes of spermatangial development in the Rhodymeniales: (1) the “separate type,” where the parent cells are separate from each other, the parent cell and spermatangia are surrounded by a common gelatinous wall, and the spermatia produced are comparatively large; and (2) the “seriate type,” in which the parent cells originate from the same cortical cell in seriate rows and are pit connected to each other, the spermatangia and the parent cell each have an independent cell wall, and the spermatia

Table 1.—Comparison of the new species of *Chrysomenia* with: A.) the morphologically similar species of form-group 1; and B.) the other known species of the tropical Western Atlantic.

	Habitat	Degree of flattening	Branching pattern	Branch constrictions	No. cortical cell layers
A. Form-group 1					
<i>C. enteromorpha</i> (1, 2, 3)	Deep, 15–90 m	Terete	Radial, commonly whorled from distal end of axial segments	+	1
<i>C. grandis</i> (4)	Deep, 30 m	Subcylindrical to slightly compressed	Simple or irregularly branched	No	
<i>C. halymenioides</i> (2, 5)	Deep, 43 m	Sub-terete to compressed	Dichotomous	Slight at most	Several
<i>C. littleriana</i> (3)	5–15 m	Compressed	Oppositely pinnate	Slight at most	3
<i>C. nodulosa</i> (3)	Deep, 17–24 m	Compressed	Alternate to oppositely pinnate	Slight	2 to 3
<i>C. ventricosa</i> (Med.) (6)	Shallow to 130 m	Terete	Alternate to oppositely pinnate	No	Several
<i>C. ventricosa</i> (Carib.) (1, 2)	Deep, to 90 m	Compressed below, terete above	Irregularly alternate to opposite	Slight	Several
<i>C. wrightii</i> (7, 8)	Shallow	Terete	Radial, alternate, opposite or irregular	+	1 to 3
B. Other tropical Western Atlantic species					
<i>C. agardhii</i> (1, 2)	Shallow to deep, to 29 m	Flat	Dichotomous to palmately lobed	No	1 to 2
<i>C. planifrons</i> (1, 2)	Deep, 30 m	Flat	Irregularly lobed	No	1

1) Børgesen 1920, 2) Taylor 1960, 3) This study, 4) Okamura 1933, 5) Harvey 1853, 6) Kuckuck 1912, 7) Lee 1978, 8) Ben Maiz et al. 1987.

Table 1.—Extended.

No. medullary cell layers	Gland cells	Hollow	Presence of medullary filaments	Distribution	Tetrasporangia	Cystocarps	Spermatangia
1	Scattered or small groups	+	—	Bermuda, North Carolina, Florida, U.S.V.I., Brazil, P.R.	Elliptical, scattered, 28 × 39 μm	Projecting	
	+	+		Japan	Elliptical, 10–15 μm	Small, roundish, not prominent	
4 to 5	+	+		Bermuda, Florida, Jamaica, Netherlands Antilles	Spherical to elliptical	Rounded, conical	
2 to 3	Occasional, mostly solitary, on medullary cells	+	+	Martinique, Guadeloupe	Elliptical, scattered, (12.5–)16 × 25 μm	Conical, projecting to 1.2 mm diam.	Average 2.4 μm diam., spermatangia in periclinal seriate series
3	Abundant on medullary and submedullary cells	+	+	Puerto Rico	Oval, scattered, 28–38 × 14–20 μm	Hemispherical, projecting to 1 mm diam.	Average 2.7 μm diam., spermatangia in anticlinal seriate series
2 to 3	Numerous, scattered	+	+	Morocco, Mediterranean	Elliptical, scattered, 20–26 × 15–19 μm		
2 to 3	Occasional, solitary; oblong	+	+	U.S.V.I., Bermuda, Jamaica, Venezuela	Elliptical, scattered, 20 μm	Hemispherical, projecting	
3 to 5	Aggregated or solitary	+	+	Japan, Korea, Mediterranean	Spherical to elliptical, 38–42 × 48–53 μm	Projecting, 850–950 μm diam.	2.9 × 4 μm, spermatangia in anticlinal seriate series
2	Occasional, scattered	+	+	North Carolina, Florida, Bermuda, U.S.V.I.	Spherical, 27 μm		
1 to 2	Occasional, scattered	+	+	Florida, Puerto Rico, U.S.V.I., Netherlands Antilles			

are comparatively small. The nature and development of spermatangia in *Chrysomenia* have been little studied and are known for only three species (Table 1). Spermatangial production for both new species is the seriate type (Figs. 9, 10), similar to that reported by Lee (1978) for *C. wrightii*, with the outer cortical cells cutting off up to 4 spermatangial parent cells. In *C. nodulosa*, the spermatangia are cut off serially from spermatangial parent cells in anticlinal rows (Fig. 9). In contrast, spermatangia are cut off periclinally in *C. littleriana* (Figs. 10, 14). As spermatangial thalli are discovered and described for other species of *Chrysomenia*, the different kinds (separate vs. seriate, and periclinal vs. anticlinal; Table 1) should be correlated to see if these characters have any taxonomic significance, perhaps for use in subgeneric groupings as has been proposed for *Gracilaria* by Yamamoto (1978).

Chrysomenia nodulosa and *C. littleriana* are unique among Caribbean species of the genus (Table 1), and distinct from all the other species of morphological form-group 1 (as noted in the Introduction). Both new species lack the totally terete thallus with the highly constricted branches as seen in *C. enteromorpha* (Børgesen 1920). They are also easily separated from *C. halymenioides*, which is dichotomously branched.

Chrysomenia nodulosa and *C. littleriana* could be confused with *C. ventricosa* sensu Taylor (1960:460, see e.g., pl. 62:fig. 3). However, on close examination, the two new species are clearly different from it in several respects. *Chrysomenia nodulosa* differs from all known species of *Chrysomenia* (Table I) in having abundant, nodulose projections irregularly scattered across its thallus surface (Figs. 2a, b, 4). It also possesses more elongate and larger tetrasporangia, as well as having branches that are more constricted at their origin than in specimens of *C. ventricosa* (MICH; US). *Chrysomenia littleriana* branches to 3–4(–5) orders vs. 1–3 orders for *C. ventricosa*. The branches of *C. littleriana* are considerably more closely set

and have broadly obtuse branch apices, and the tetrasporangia are smaller and more elongate than those of *C. ventricosa*. Furthermore, the distal portions of the thalli are compressed in *C. littleriana* and *C. nodulosa*, whereas they are terete in *C. ventricosa*.

Of the non-western Atlantic species, *Chrysomenia wrightii* superficially resembles *C. nodulosa*; however, *C. wrightii* differs in possessing terete axes and up to five layers of medullary cells (Lee 1978, Ben Maïz et al. 1987). These characters also serve to differentiate *C. littleriana* from *C. wrightii*.

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